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GEOGRAPHIC ORIENTATION, TIME AND MUDSNAIL PHOTOTAXIS

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A series of investigations of mudsnails in our laboratories led to the conclusion that these snails were remarkably sensitive to the atmospheric electromagnetic fields. They exhibited orientational modifications in response to experimentally altered directions and strengths of very weak magnetic fields (Brown, Brett, Bennett, and Barnwell, 1960; Brown, Bennett and Webb, 1960; Brown, Webb, and Brett, 1960; Barnwell and Brown, 1961; Brown, Webb, and Barnwell, 1964). Indeed, there appeared to be solar day, lunar day, and semimonthly variations in their responsiveness to specific parameters of such fields. Not only was their responding mechanism geared to deal most effectively with fields very close to natural ambient strengths, but the snails were able to adjust or accommodate in a short time and then respond well to an experimentally altered strength (Brown, Barnwell, and Webb, 1964). Systematic variation in magnitudes of responses to horizontal magnetic fields with vector directions parallel and at right angles to their bodily axis in a fixed geographic orientation led to a hypothesis that the responding system was acting as a directional dual antenna (Brown, 1960). The snails were behaving as if one component was rotating within the body in a manner correlated with the earth's rotation relative to the sun, and the other component, relative to the moon.

Other experiments strongly suggested that the snails could also perceive and distinguish directional vectors, separately, of the electrostatic field (Brown, Webb and Schroeder, 1961) and high energy radiation (Brown, and Webb, 1968) of their environment. Comparable studies with the flatworm, *Dugesia,* suggested that such biological responsiveness was widespread (Brown, 1971).

The present investigation was designed in order to learn more concerning the natural behavior of the snails as it varied with time of day and month, and with four geographic orientations, and to discover any other systematic variations which might be present. It seemed probable that further information concerning biological clocks and geographic orientation would be disclosed. With the remarkable similarities in clock and compass phenomena throughout the spectrum of life, any discoveries in the mudsnail would be expected to extend our knowledge of the basic nature of the phenomena in organisms in general.

Materials and Methods

The abundant marine mudsnail, *Nassarius obsoletus*, was obtained during each of four summers from a single small tidal area in Chappoquoit Marsh, West Falmouth, Massachusetts. About 300 animals were collected twice each week, Mondays and Fridays, with each collection kept separate on tables in running sea water. During the first year (1972), the experiments were performed in a second-floor room with southerly exposure in the Lillie Building at the Marine Biological Laboratory. The stocks were maintained on a lead-lined sea table. The remaining studies (1974, 1975 and 1976) were conducted in two different but similar laboratories with southerly exposure, on the second floor of Whitman Building, with the collections maintained on fiberglass sea tables. The rooms were air-conditioned to essentially constant temperature. In 1976, for example, the early AM temperatures averaged $20.6 \pm 0.7°$ C; and the PM ones, $21.4 \pm 0.8°$ C. The snails collected on Mondays were observed in experiments the following Thursdays and Fridays; those collected on Fridays were observed the following Mondays, Tuesdays, and Wednesdays. After use each collection of snails was discarded.

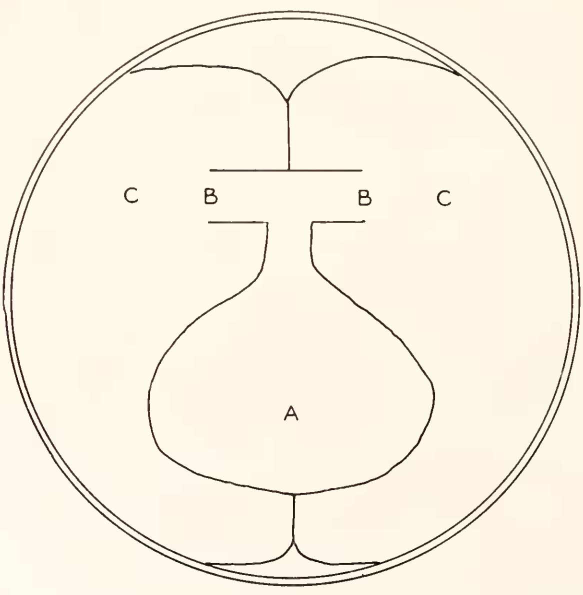

FIGURE 1. View from above one of four identically constructed orientation chambers for the snails—a 23 cm cylindrical glass crystallizing dish with an aluminum frame inserted. The snails initially placed in A make their way out through B into C.

The experiments comprised picking at random forty snails from the stock supply and placing ten in each of four special containers, constructed to be as closely identical as possible. These containers were cylindrical glass crystallizing dishes 23 cm in diameter with vertical 8 cm sides, containing aluminum inserts made from 40 × 10 cm sheets folded in half lengthwise, the two halves freed from one another by a cut close to the fold except over two short sections, and then given the form noted in Figure 1. Continuity at B in the figure was accomplished by leaving the upper half of each side uncut to produce an escape passage about 2.5 cm in height. These inserts were held firmly in place by the spring of the metal. The neck of the center corral, A, was kept with constant width by a small aluminum saddle.

One such container was placed in each of four plywood boxes with light-tight but easily removable covers. The exits for the starting points (A in Fig. 1) for the snails were directed in each of the four cardinal compass directions. When covered, the snails received illumination only from their right or their left from a 25-Watt frosted lamp by way of 3 cm circular apertures in the box at right angles to the path of the snails as they were ready to exit. Exiting snails went in large majority toward the light, whichever side it chanced to be, indicating a persistent, moderately strong, positive phototaxis.

Each morning, five days a week, between about 7:30 and 9:30, and again each afternoon between about 12:30 and 14:30 Eastern Standard Time, every dish of ten snails was exposed for a carefully measured ten minutes apiece to each of eight conditions: pointed in each of the four directions with the light on the right side and with the light on the left side. The number of snails that had emerged into C of Figure 1, toward the light and away from it, for each light direction was recorded. The containers with their snails were then moved and observed again in different geographic directions in opposite rotational direction between one day and the next. The order of offering the lights, right and left, also alternated between days.

The data for each half day thus contained as the mean for the forty-snail sample, the differing degrees of tendency to move, the differing tendencies of snails to emerge among the four compass directions, and the differing strengths of the phototactic response. The snails, when moving (rate ranged from 0.14 to

TABLE I

Diurnal differences in number of snails active.

Year	Mean number emerging		PM as % of AM	Number of days		Number of days
	AM	PM		AM > PM	PM > AM	
1972	83.8	70.8	84.5	26	18	44
1974	208.1	167.4	80.4	42	8	50
1975	163.5	134.1	82.0	45	13	58
1976	179.1	150.9	84.3	39	11	50
Mean	158.6	130.8	82.8			
Sum				152	50	202

0.23 cm/sec) could easily reach C of Figure 1, and the shape of the corral prevented snails from re-entering B during the ten minutes.

Any unintentional bias introduced by differences between specific boxes or specific lights was minimized by complete shuffling of the boxes among directions and also the light bulbs of the boxes between one year and the next.

The experiments were conducted on 44 days in 1972 (June 26 through August 24), 50 days in 1974 (June 17 through August 23), 58 days in 1975 (June 10 through August 28) and 50 days in 1976 (June 14 through August 20). The maximum total possible number of snail exits for AM or PM, over the four years was 64,640 with 8080 different snails, or 320 per half day for 40 snails for 202 days.

Results

All snails

There was a mean diurnal variation in the total number of snails emerging. For each of the four summers only about 83% as many snails emerged into C (Fig. 1) in the afternoon as in the morning (Table I). The consistency of this ratio among the four years emphasized the high statistical significance which is also evident from an examination of the number of days on which more emerged in the morning than afternoon ($\chi^2 = 51.5$, d.f. = 1, $P < 0.001$). There appeared to be no significant difference between the percentages of animals responding negatively to the light between AM and PM. The mean for afternoon for the four years was about 96% of morning. However, there were highly significant differences among the four years in the mean daily percentage of negatively phototactic snails (Table II). The latter percentages tended to be negatively correlated with the number of active snails ($r = -0.91$, $t = 3.04$, $P < 0.06$).

The day by day differences in total numbers of snails emerging between morning and afternoon for each of the three years of study in the Whitman Building (1974, 1975 and 1976) appeared to display a mean, essentially bimodal, synodic monthly variation. The minima tended to fall four to five days following both new moon and full moon. Analysis of variance of four successive segments of the month (7, 10, 6, and 7 days commencing at new moon) yielded $F = 9.19$, d.f. = 3, and $P < 0.001$. The pattern of this mean synodic monthly cycle for the data for the three years (Fig. 2) coincided remarkably with the mean synodic monthly cycle of water uptake of pinto bean seeds during their first four hours (over the noon hour) in water as found by two observers independently assaying daily the

Table II

Average number of snails active per day and percentages of negatively phototactic snails.

Year	Mean daily % negative	Mean number active/day
1972	18.05 ± 0.919	154.6
1974	10.62 ± 0.502	375.5
1975	12.90 ± 0.493	297.6
1976	8.40 ± 0.414	330.0

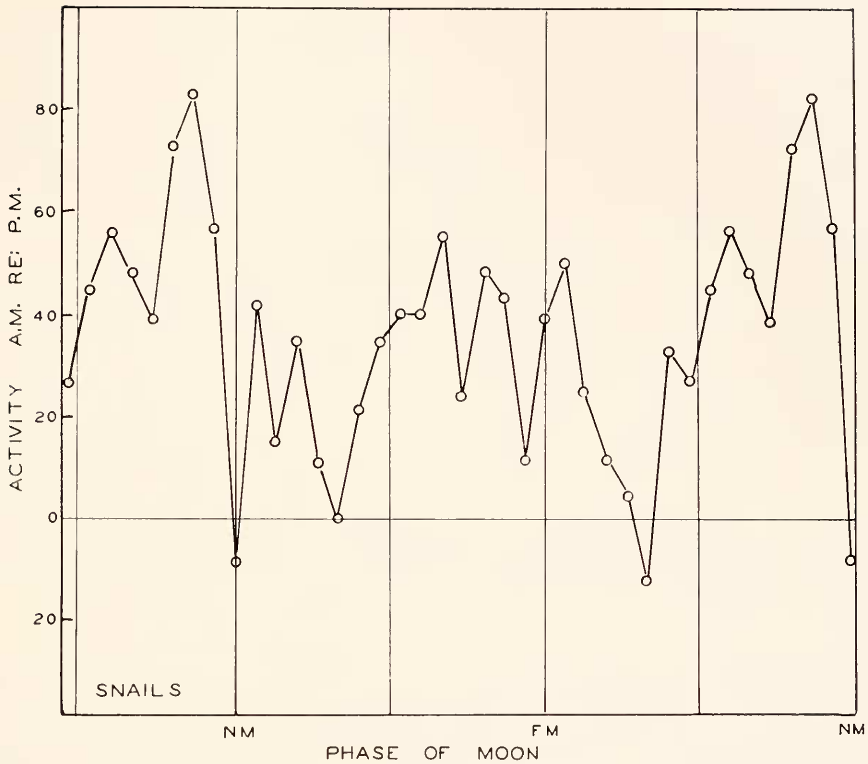

FIGURE 2. The mean differences in numbers of active snails between AM and PM for days of the synodic month for the three summers, 1974 through 1976; NM is new moon; FM, full moon.

water uptake (percentage weight increase of the beans) as averages of 32 twenty-bean samples concurrently in the same laboratory during the summer of 1976 (Fig. 3). The similarity between these snail and bean synodic monthly cycles was interpreted to render it improbable that the snails had obtained this cycle from the periodism of the tides on the beach from which they had been collected three to five days earlier and thereafter were maintaining the cycle autonomously by some endogenous oscillating system. Moreover, a comparison of the mean monthly variation of the same AM–PM difference for the snails during 1972 with that for the data of Figure 2, taking ten independent consecutive three-day means of each to compensate for the paucity in data comprising the 1972 cycle, yielded $r = -0.647$, $N = 10$, and $P < 0.05$. The 1972 monthly pattern was approximately mirror-imaging that found for the later three summers.

Negatively phototactic snails

Examination of the mean monthly patterns of variation in the percentage of negatively phototactic snails for all data for each of the two halves of the day

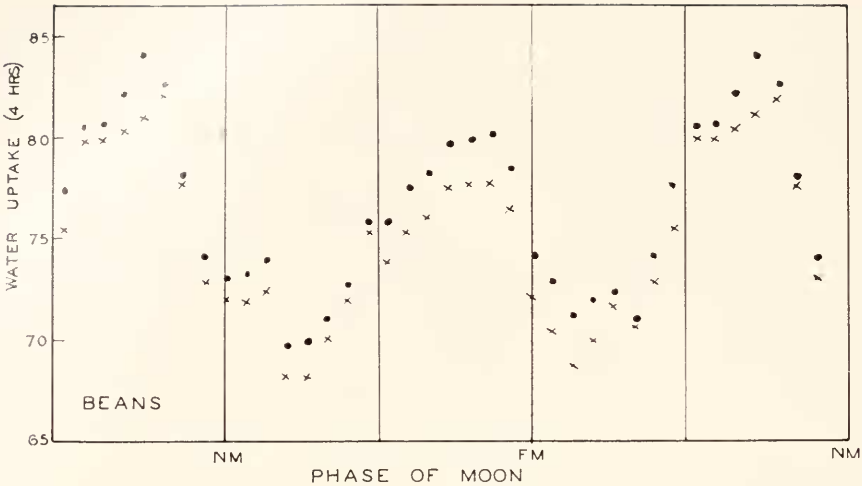

FIGURE 3. The monthly variation in 1976 in increase in weight of Pinto beans by water absorption over a carefully measured four-hour interval, as measured by two observers in the same laboratory at the same times at which the snails were being studied. These are three-day moving means; NM is new moon; FM, full moon.

disclosed these to be moderately similar to one another. The coefficient of correlation between the two independent AM and PM series was +0.636, t = 4.37, N = 30, and $P < 0.001$. The mean monthly pattern for the averaged AM and PM percentages for the four years was negatively correlated with the four-year mean monthly pattern of all emerging snails, with r = −0.51, t = 3.14, N = 30, and $P < 0.005$. An analysis of variance for the percentages of negatively phototactic snails using both AM and PM patterns for four successive segments of the month (12, 5, 8, and 5 days commencing the sixth day following full moon) yielded F = 4.77, d.f. = 3, N = 60, and $P < 0.01$. Two minima were evident and occurred in the same lunar relationships as shown in Figure 2. The ranges of three-day moving means were 38% and 57% of the averages for AM and PM, respectively.

Of great importance was the fact that no single year of data even remotely suggested positive correlation between the AM and PM patterns. The similarity gradually became evident with the increasing years of accumulated data, strongly suggesting that the similarity appeared as a common, specifically patterned, monthly variation which became apparent only with reduction of noise with the increasing amounts of pooled data.

During investigation of the numbers of negatively phototactic snails for each compass direction a highly significant difference was found among them. As seen in Figure 4, the minimum negative behavior was noted when the snails were directed east with light from north or south. A maximum in negative responses was observed for south-directed animals with illumination from the east or west. The coefficient of correlation, r, between the geographic morning and afternoon patterns for the four years (Table III) was +0.872, t = 6.66, N = 16, and $P < 0.001$. This last high correlation also incorporated the significant differences among the years in total activity. A χ^2 test for the difference between the totals for the east and south negative responses yielded 14.7, d.f. = 1, and $P < 0.001$. For AM and PM separately, the differences gave $\chi^2 = 7.72$ and 6.99, respectively, with $P < 0.01$ for each. In the combined data for AM and PM, north and east differed from south and west, $\chi^2 = 16.36$, d.f. = 1, and $P < 0.001$. Clearly, the effect of the illumination in orienting the snails varied with the compass direction of the paths as the snails encountered the right-angle lights from their right or left sides.

Another analysis was made for all the data on snails that had responded negatively to the lights. First, comparing all the negative responses when the light was from the left, numbering 3306, with those when the light came from the right, numbering 2974, yielded a χ^2 of 17.55, d.f. = 1, and $P < 0.001$. The same difference was evident for both AM ($\chi^2 = 9.58$, $P < 0.01$) and PM ($\chi^2 = 7.98$, $P < 0.01$) separately. The negative response was, on the average, about 11.1% stronger when the light was from the left than when from the right. However, this percentage

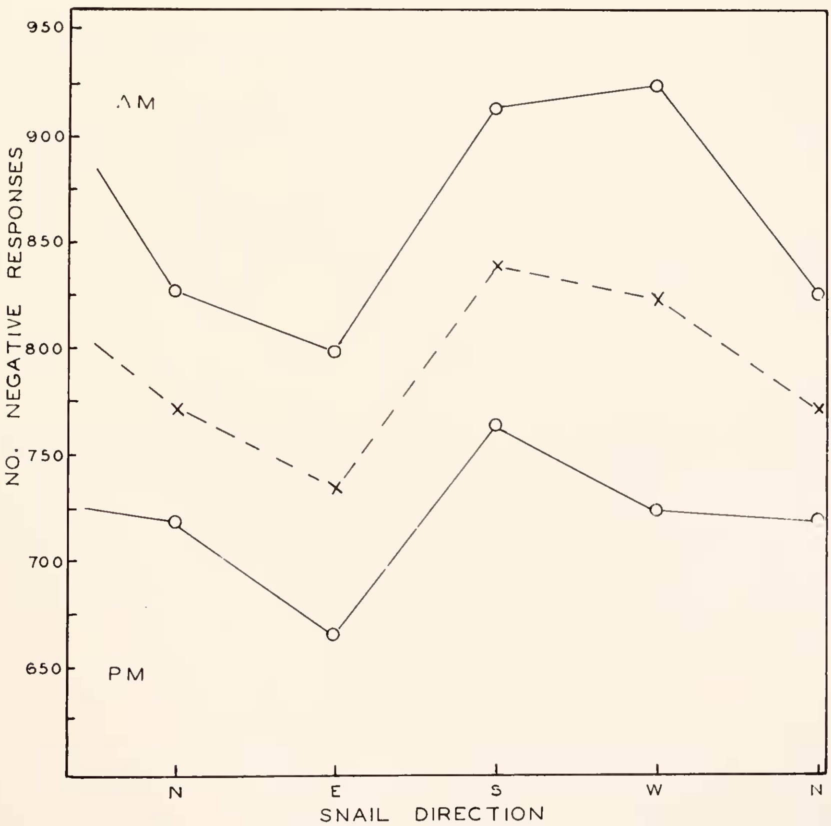

FIGURE 4. The numbers of negatively phototactic snails emerging for each geographic direction for AM and PM over the four summers of study. Abscissa indicates the direction of snail movement upon encountering a light from the right or left. The broken line describes the means for AM and PM.

TABLE III

Numbers of negatively phototactic snails.

	Year	N	E	S	W
AM	1972	137	143	195	165
	1974	212	214	245	252
	1975	306	287	315	307
	1976	171	155	159	201
				Total: 3464	
PM	1972	113	124	167	117
	1974	228	183	215	201
	1975	226	197	222	252
	1976	151	161	161	156
				Total: 2874	

varied systematically with compass direction. In the mornings this was greatest for north-directed snails (29.5%) and least for east-directed ones (−3.8%). It was 3.3% for south and 6.4% for west. Afternoons, quite differently, it was greatest for south-directed snails (19.1%) and least for north-directed ones (5.3%). The remaining directions gave intermediate values, 11.0% for east and 6.4% for west. The afternoon maximum in preference for the left over the right light had shifted about 180° relative to the morning maximum. Correlating the two half-day patterns of relative strengths of negative response with one another yielded a statistically significant correlation only with a 180° phase shift between them ($r = +0.956$, $t = 4.61$, $N = 4$, $P < 0.02$).

Positively phototactic snails

Even more striking findings from this study came from an analysis of the choices among the geographic directions. Expressing the total positively photo-tatic emergences for each direction as percentages of the total emerging with positive phototaxis for each half day, the values could be exprssed as deviations from 25%. This resulted in four intercorrelated values for each half day but fully independent values between AM and PM. It was evident that the variances were greater among directions in the afternoon than morning (Table IV) for each of the four years. For the pooled data the significance was great ($N = 808$, $P < 0.001$).

TABLE IV

Variances among directional choices.

Year	Var. AM	Var. PM	F_{max}	N	P
1972	15.704	23.422	1.491	176	<0.01
1974	13.869	19.332	1.394	200	<0.01
1975	22.629	32.884	1.453	232	<0.01
1976	17.479	20.490	1.172	200	<0.20

Table V

Deviations of mean paths from 25.00%.

	Year	N	E	S	W
AM	1972	−1.97	+0.22	+1.28	+0.72
	1974	−0.02	−0.52	+0.23	+0.30
	1975	−0.54	+1.30	−0.75	−0.27
	1976	−0.96	−0.05	+0.63	+0.47
		−0.87	+0.24	+0.35	+0.31
PM	1972	−2.92	+5.48	−0.33	−2.38
	1974	−0.32	+0.13	+0.63	−0.47
	1975	+0.53	−0.87	+0.03	+0.38
	1976	−0.94	+1.33	+0.48	−0.75
		−0.91	+1.52	+0.20	−0.81

A most novel discovery, however, arose from an attempt to demonstrate a correlation between the mean patterns of directional choices for mornings with afternoons. An inspection of the data for the summer of 1972 had suggested that no correlation existed between the mean morning and afternoon values direction by direction (Table V, Fig. 5A), but that a positive correlation was suggested between the directional patterns for the two times of the day when the afternoon pattern was displaced clockwise (from above) by 90° (Fig. 5B). A significant negative correlation occurred for a 270° displacement (Table VI). In viewing the data for the next three years, it was discovered that there was a positive correlation of the same general magnitude for each year between the morning patterns and the afternoon ones after a 90° clockwise displacement of the latter ($r = +0.677$, $t = 2.926$, $N = 12$, $P < 0.004$) despite no correlation between the same directions ($r = -0.155$, $t = 0.279$, $N = 12$). Because of the correlated nature of the four directional values the remaining two degrees of rotation, 180° and 270° would be expected to average a negative value. A 180° phase shift of the PM values yielded $r = +0.009$, $t = 0.028$, $N = 12$, and a 270° shift gave $r = -0.535$, $t = 2.00$, $N = 12$. When the 1972 data were included, the corresponding r-values were those listed in Table VI.

Table VI

Coefficients of correlation, r, between AM *and* PM *patterns.*
PM *patterns shifted clockwise relative to* AM *ones.*

Phase shift CW	1972	1974	1975	1976	All years
0°	+0.295	−0.104	−0.877	+0.340	−0.176
90°	+0.660	+0.715*	+0.646	+0.794	+0.616***
180°	+0.021	+0.357	+0.182	−0.171	+0.043
270°	−0.976**	−0.968**	+0.048	−0.963**	−0.811****

* $P < 0.05$ for pooled 1972–74; ** $P < 0.01$; *** $P < 0.005$; **** $P < 0.001$.

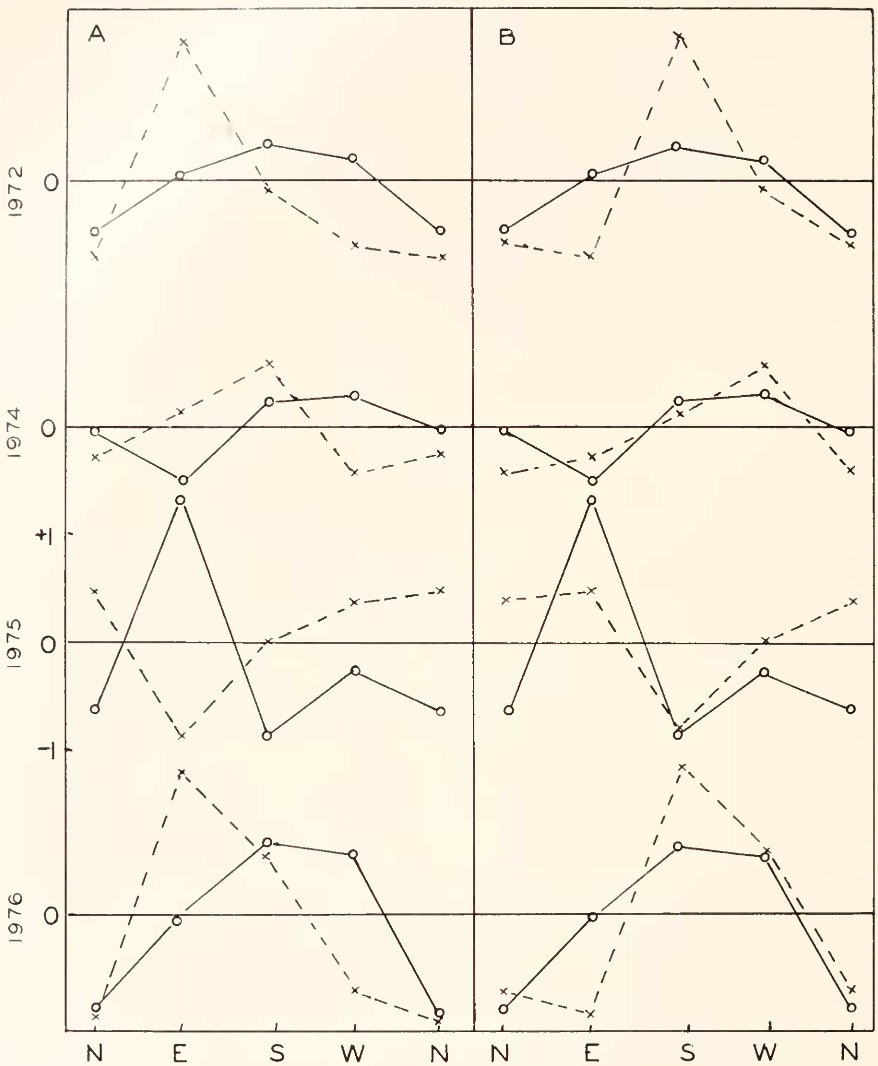

FIGURE 5. The directional preferences of snails during four years, mornings (solid line) and afternoons (broken line). The 1972 patterns are plotted at 25% of the range of the others. The ranges are shown as percentage points on the 1975 ordinate: A, all geographic directions as shown on abscissa, and B, AM values as shown on abscissa; PM values all shifted 90° clockwise (from above).

It seems significant that a maximum positive correlation and a maximum negative correlation for the four years are 180° apart (90° and 270°), and both were found to be significantly different, as means, from the noncorrelated values found for 0° and 180°. This suggests that it is not simply a directional preference but an axial preference which is shifting counterclockwise 90° between AM and PM.

Except for the year 1975 the tendency to select one geographic direction is associated with a tendency to avoid the opposite direction. It is unfortunate that the study could not have included 1973; possibly a similar anomaly to 1975 might have occurred, suggesting that the phenomenon alternated between one year and the next.

Discussion

The snails exhibited a mean 24-hour variation in essentially the same relation to time of day throughout all four summers that they were studied. This was easily explained since the snails experienced the natural day-night changes of the laboratory. This daily cycle included a relatively uniform mean reduction in activity between morning and afternoon and the difference, in turn, showed a bimodal synodic monthly pattern of modulation through 1974, 1975 and 1976. A close similarity of this pattern to that of bean water absorption occurring in the same laboratory during the summer of 1976 pointed to a subtle exogenous origin.

The mean monthly patterns of the snails through the five-year span of this study tended significantly to display a common bimodal form with minima occurring between new moon and first quarter and between full moon and third quarter. However, for some measured parameters, or at certain times, a monthly pattern for the snails was registered which was negatively correlated, with high statistical significance, with the more typical one. Minima and maxima had exchanged places. Inversion of geophysically dependent patterns including both lunar day and monthly ones has been reported between different species, within a single species at different times, and even concurrently within a single species under slightly different experimental conditions (Brown, 1960; Brown and Chow, 1973, 1976). Such inversions comprise a phenomenon which is probably commonplace. It is postulated that the inverting tendency reflects the organisms' sign and strength of response to an effective atmospheric factor which is capable of being altered, even tipped between positive and negative, with changing physiological state of the organism and by effects of other uncontrolled, or imposed, environmental conditions. Indeed the sign has been described to differ between one portion of a lunar or solar cycle and another (Brown, 1960; Brown, 1962b).

The similarity of the four-year mean monthly patterns found for the negatively phototactic snails between AM and PM, together with the absence of any comparable similarity between these patterns for the single years, bespeaks a continuing input to the snail population of a detailed exogenous, noisy, monthly pattern. This can be compared in principle with the reproducible low amplitude bimodal monthly patterns of modulation of a circadian rhythm observed for hamsters during a two-year study (Brown and Park, 1967). A common mean residual pattern, differentiating specific days in a lunar month must have persisted throughout this study. The highly significant correlation denies random monthly sequences of points.

The variation in strength of negative phototaxis with differing geographic direction of movement of the snails suggests within the animals an interaction between the oriented visible light and a polarized, subtle geophysical field within the test chambers. The latter field is presently postulated to be geomagnetism, the most regular of those known to which snails are responsive. Significant synergistic interactions between an overt vector field such as light and a vector atmospheric electromagnetic field such as geomagnetism has great implications for behavior in general.

They suggest an area for future investigations in receptor and sensory physiology and perception more broadly among organisms.

The negative responses of the snails differed between right and left lights. The response was stronger to a light on the left than on the right. This could not be due exclusively to shell coiling inasmuch as the magnitude of the difference varied systematically with the geographic direction of the snails as they encountered the lights. The pattern of this differential responsiveness with geographic direction was also 180° shifted afternoons relative to mornings. Such behavior resembles the essential inversion of the geographic directional pattern of response to a weak, right-angle, horizontal electrostatic field between morning and afternoon by the planarian, *Dugesia* (Brown, 1962a).

Among the four years the compass pattern of directional choices differed between one year and the next. But despite this, the afternoon patterns most closely resembled the morning ones each year when displaced 90° clockwise. The only manner in which these and other discovered results could be obtained is that the snails possess a system integrating the temporal daily cycle with the two-dimensional geographic compass one. Between AM and PM the patterns of directional preferences had shifted about 90° counterclockwise in the geographic compass cycle. This behavior is consistent with the earlier findings that snails could not only distinguish horizontal vector direction of magnetism but that they behaved as if a major sensor system for magnetic field rotated in a manner geared to the relative movements of sun and earth even when the sun was not visible.

The approximate quarter-cycle counterclockwise directional, or axial, preference shift between AM and PM would be an expected consequence if a sensor for magnetic vector direction relative to the longitudinal body-axis were, in effect, rotating clockwise once a day within the organism in response to an atmospheric parameter complex, reflecting the apparent clockwise motion of the sun in the northern hemisphere. To maintain a given compass orientation of its rotating sensory mechanism to the geomagnetic polarity, which especially in the absence of the sun appears to be a major orienting factor for organisms (Wiltschko and Wiltschko, 1972; Emlen, Wiltschko, Demong, Wiltschko, and Bergman, 1976), the organism must be shifting its angle of orientation relative to the geomagnetic field at a rate of 360° per day, or about 90° counterclockwise between morning and afternoon as discovered herein. It is postulated that the mechanism of clock compensation for the motion of the sun across the sky relative to the magnetic polarity of the earth is reflected here. Under the controlled conditions of this experiment, with a single fixed light with direction neutralized by equal right and left exposures, this becomes evident. Normally, with a view of the sun available for directional reference, this system would enable a consistent geographic direction to be maintained as a sun-compass response. In the absence of view of the sun and with neutralized direction of artificial lights the orientation of the organism relative to a residual stationary directional field such as geomagnetism rotates steadily counter-clockwise.

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Summary

1. Mudsnails, *Nassarius obsoletus,* collected at Chappoquoit marsh, West Falmouth, Massachusetts, were observed in apparatus designed to assay samples of forty snails both mornings and afternoons for their activity, directional preference, and sign and strength of phototaxis.

2. Assays were made during two to three months over each of four summers (1972, 1974, 1975 and 1976).

3. Activity was less, and variances among choices of directions was greater, during afternoons than mornings.

4. A mean monthly pattern was described for the difference between AM and PM activities for all snails; for only negatively phototactic snails a comparable monthly pattern for AM was highly significantly correlated with one for PM. The monthly pattern of negatively phototatic snails *negatively* correlated with the monthly pattern of total snail activity.

5. The strength of negative phototaxis, as well as differential influences between right and left lights, differed with geographic oriention of the snails and indicated an integration within the snails of response to light and to a horizontally polarized subtle geophysical field.

6. For positively phototactic snails a highly significant positive correlation between the AM and PM patterns of directional choices occurred only when PM compass patterns were rotated 90° clockwise relative to AM ones, with a similarly highly significant negative correlation occurring for 270°.

7. This 90° shift is interpreted to result from orientation to geomagnetism employing a "rotating magnetic sensor" in the snails which is normally used for sun-compass compensation.

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